Chapter

Sustainable Strategies for Managing Bacterial Panicle Blight in Rice

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Abstract

Bacterial panicle blight (BPB) is present in more than 18 countries and has become a global disease in rice. BPB is highly destructive and can cause significant losses of up to 75% in yield and milling quality. BPB is caused by *Burkholderia glumae* or *B. gladioli*, with the former being the primary cause of the disease. Outbreaks of BPB are triggered by conditions of high temperatures in combination with high relative humidity at heading. The disease cycle starts with primary infections from infected seed, soil, and irrigation water, and subsequent secondary infections result from rain splash and panicle contact. Limited management options are available for control of BPB. There are only several cultivars including hybrids with partial resistance available currently. Twelve quantitative trait loci (QTLs) associated with the partial resistance have been identified. Oxolinic acid is an effective antibacterial compound for control of BPB in Japan, but it is not labeled for use on rice in the USA and many other countries. Sustainable control of BPB relies on integrated use of available management strategies of exclusion, genetic resistance, chemical control, biocontrol, and cultural practice. Developing and use of resistant cultivars is the best strategy to minimize the damage caused by BPB and maximize rice production in the long term.

Keywords: rice, bacterial panicle blight, seedling rot, grain rot, QTLs, *Pseudomonas glumae*, *Burkholderia glumae*, *Burkholderia gladioli*, disease control, IPM, epidemiology, genetic resistance, chemical control, biocontrol, cultural practice

1. Introduction

Bacterial panicle blight (BPB), caused primarily by *Burkholderia glumae*, has become a threat to rice production globally. BPB has the potential to cause significant losses in grain yield and milling quality in epidemic years. The disease causes several types of damage, including seedling blight, sheath rot, floret sterility, grains not filling or aborted, and milling quality reduction, resulting in a reduction of yield by up to 75% [1–4]. In Japan, BPB has become one of the major rice diseases. Severe outbreaks of this disease occurred on more than 69,000 ha in 2013 and 30,000 ha in 2015 [5, 6]. In the USA, BPB has recently become as one of the most important diseases in rice in terms of economic importance. A survey found that the disease was present in approximately 60% of Louisiana rice fields [7]. In the Southern USA, significant yield losses from BPB were reported in 1995, 1996, 1998, 2000, 2010, and 2011 [1, 8–11]. In Louisiana, yield losses for severely infected fields reached 40% in

1995 and 1998 [1, 8]. In Arkansas, BPB was so severe in 2010 that yield losses were estimated at 50% in susceptible cultivars [9]. In Texas, the outbreaks of BPB resulted in an estimate of 10–20% yield loss in the Texas Rice Belt in 2010 [10, 11]. Outbreaks of this disease also occurred in rice under organic production systems in 2010 in Texas [11]. In the disease-yield loss field study, we found BPB was highly destructive and could cause yield losses ranging from 1 to 59% (83–4883 kg/ha), with yield loss increasing approximately 5% (455 kg/ha) for every unit increase in BPB severity on the rating scale of 0–9 [12]. Based on annual rice production in the Mid-South USA in 2003–2013, it is estimated that BPB caused $61 million USD of damage that would feed 1.1 million people annually (Aaron Shew, personal communication).

Effective management of BPB is critical to minimizing the damage caused by the disease and maximizing production returns. However, limited options for management of the disease are available currently. No single genes or quantitative trait loci (QTLs) for complete resistance to BPB have been found so far [13, 14]. Only a few rice cultivars with partial resistance are available for commercial use. No chemical control options are available in the USA although oxolinic acid has been used as a major control measure for BPB in Japan for more than two decades [15]. Resistant populations of *B. glumae* to oxolinic acid have been found [16–19], which limits increasing use of this antibiotic compound for management of BPB. Oxolinic acid is not labeled for use on rice in the USA and many other countries. Compared to extensive research and significant advances made on management of sheath blight caused by *Rhizoctonia solani* and rice blast caused by *Magnaporthe oryzae*, very limited research has been conducted on the development of effective and sustainable management options for control of BPB.

In this article, we focus on the review of recent advances on the development of management strategies for BPB, including exclusion, genetic resistance, chemical control, biological control, and cultural practice. In addition, world distribution of the pathogen, characteristic symptoms of BPB, and current understanding of epidemics of BPB are also included. Two review articles covering the pathogenesis of *B. glumae* and the detection of BPB have been published previously [20, 21]. The terms “BPB” and “grain rot” have been used interchangeably in the literature. However, BPB has been commonly used in the USA and Latin America, while grain rot in Japan and other countries [20]. The term BPB is used in this review article.

2. Pathogens

Since the first description of *Burkholderia glumae* (formerly *Pseudomonas glumae* Kurita and Tabei) as the bacterial pathogen causing rice seedling rot and grain rot in Japan in 1955 [22], BPB has been reported in more than 18 countries distributed in Africa, Asia, Latin America, and North America (**Table 1**). The total rice production from these countries accounted for more than 65% of total world rice production in 2018 [23]. BPB has become an increasingly important global disease in rice. In addition to *B. glumae*, *B. gladioli* has also been identified as another bacterial pathogen causing the BPB disease. Infection with *B. gladioli* produces the same symptoms as infection with *B. glumae*. The disease caused by *B. gladioli* has been reported in Arkansas (USA), China Japan, Louisiana (USA), Panama, and the Philippines, where *B. glumae* is also co-present (**Table 1**). In the USA, the cause of the BPB was not known at the time when epidemics of BPB occurred in 1995. In 1996–1997, however, when evaluating bacterial isolates from rice tissue for their ability to control the rice sheath blight fungus *R. solani*, investigators in Louisiana accidentally found that some of the *B. glumae* isolates caused panicle blighting symptoms when greenhouse grown rice plants were spay inoculated [44]. This led to the discovery of *B. glumae* as the causal agent of the BPB disease.

Country	Year	BPB pathogen	Reference
Japan	1955	*B. glumae*	[22, 24]
Taiwan (China)	1983	*B. glume*	[25]
Columbia	1989	*B. glumae*	[26]
Latin America	1989	B. glumae	[26]
Vietnam	1993	*B. glumae*	[27]
Japan	1996	*B. gladioli*	[28, 29]
The Philippines	1996	*B. glume* and *B. gladioli*	[30–32]
Louisiana (USA)	2001	*B. glume* and B. gladioli	[1, 33]
Korea	2003	*B. glumae*	[34]
China	2007	*B. glumae*	[35]
Panama	2007	*B. glume* and *B. gladioli*	[36]
Nicaragua	2008	*B. glumae*	[37]
Arkansas (USA)	2009	*B. glume* and *B. gladioli*	[1, 9]
Mississippi (USA)	2009	*B. glumae*	[1]
Texas (USA)	2009	B. glumae	[1, 10]
Honduras	2011	*B. glumae*	Lex Ceamer, personal communication
Mississippi (USA)	2012	*B. gladioli*	[38]
Costa Rica	2014	*B. glumae*	[39]
Ecuador	2014	*B. glumae*	[40]
South Africa	2014	*B. glumae*	[41]
India	2015	*B. glumae*	[42]
China	2018	*B. gladioli*	[43]

Table 1.
Countries reported with the presence of bacterial panicle blight (BPB) caused by Burkholderia glumae and B. gladioli in rice as of January 2019.

BPB of rice can be caused by either *B. glumae* or *B. gladioli*. However, the former is the primary cause of the disease. The study of Nandakumar et al. [1] found that 76 and 5% of the bacterial strains collected were *B. glumae* and *B. gladioli*, respectively. In a field survey conducted in Mississippi using PCR analysis, it was found that 84% of rice panicle samples collected were positive for *B. glumae* and 12% of the samples positive for *B. gladioli* [38]. In a recent survey conducted in nine rice-producing counties of Arkansas, all 45 virulent bacterial isolates studied were *B. glumae*, and no *B. gladioli* isolates were identified [9]. In addition, the *B. glumae* pathogen tends to be more virulent and causes more damage to rice plants when compared to the *B. gladioli* pathogen [20, 33].

3. Symptoms

The symptoms of BPB include seedling blight, sheath rot, and panicle blighting [1–4]. These symptoms can be induced by either *B. glume* or *B. gladioli*. Virulent bacterial strains produce the yellow-pigmented toxin toxoflavin on King's B agar medium (**Figure 1**), while avirulent strains do not produce this toxin [1]. Production of toxoflavin is an essential factor to induce the development of the symptoms on rice seedlings and grains [34, 45, 46].

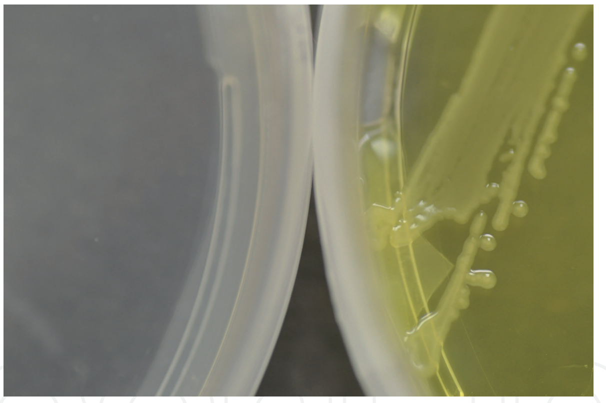

Figure 1.
Colonies of Burkholderia glumae and production of yellow pigment (toxoflavin) by B. glumae on King's B agar plate (right) vs. no pigment production control plate (left). Photo was taken at 3 days after inoculation at 30°C.

Figure 2.
A focal pattern of bacterial panicle blight (BPB) on the Presidio (cv) rice panicles (center) in a research plot inoculated with Burkholderia glumae at Beaumont, Texas.

Unlike rice sheath blight and blast, BPB is difficult to be diagnosed based on the symptoms on panicles. Similar symptoms on panicles can be caused by many abiotic and biotic factors including heat, insect damage, and secondary microorganisms [3, 4, 47]. However, BPB has the symptoms that can be distinguished from other causes. BPB occurs sporadically on individual plants or in circular or oval patterns in the field (**Figures 2** and **3**). In contrast, common panicle blanking, caused by abiotic stress such as from excessive heat, develops in the field more uniformly and does not form apparent foci. There are three important characteristics of BPB that separate it from other panicle disorders: (1) BPB often does not appear to prevent successful pollination although it can affect individual glumes or whole panicles (**Figure 4**). Thus, seed may be present on the panicle unlike panicle sterility that is caused by heat stress. (2) Infected florets initially have discoloration ranging from light green to light brown on the basal portion of the glumes with a reddish-brown margin separating this area from the rest that becomes straw-colored later (**Figures 4** and **5**). (3) The rachis or branches of the panicle remain green for a while at the base of each floret, even after the glumes desiccate and turn tan (**Figures 4** and **5**). Florets at the latest stages of infection usually appear to be gray or black due to the abundant growth of saprophytic fungi on the surface (**Figure 5**). The disease can cause linear lesions on sheaths with a distinct reddish-brown border and a gray and necrotic center, resulting in sheath rot (**Figure 6A**) and stem rot (**Figure 6B**). On the leaves, lesions are circular to oval with a smooth reddish-brown border and a gray or straw-colored center (**Figure 6C**). If the infected plants are young, this disease can cause seedling blighting (**Figure 6D**) or seeding rot. The symptoms of seedling rot were

Figure 3.
Symptoms of bacterial panicle blight (BPB) on a Presidio (cv) rice panicle head (arrow) in the field inoculated with Burkholderia glumae at the flowering stage at Beaumont, Texas.

Figure 4.
A close look at the symptoms of bacterial panicle blight (BPB) on Presidio (cv) rice panicles. Photo was taken approximately 2 weeks after inoculation with Burkholderia glumae at the flowering stage at Beaumont, Texas.

first reported in Japan [22] and frequently occur in young rice plants. However, these symptoms on leaves, sheaths, stems, and seedlings are rarely observed under the field conditions in the Southern USA [4]. This is one of the reasons why no scouting methods have been developed to detect and predict the development of BPB based on the symptoms on leaves and sheaths at the early crop growth stages.

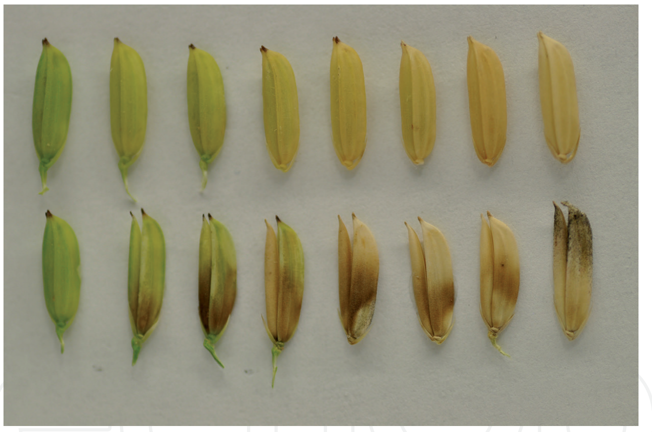

Figure 5.
Comparison of the developmental symptoms of bacterial panicle blight (BPB) on infected kernels of rice (lower row) and healthy kernels (upper row). Photo was taken for rice kernels collected from different Presidio (cv) rice plants inoculated with Burkholderia glumae at the flowering stage in the field. Note the occurrence of secondary fungal infection on the discolored kernel at the late BPB development stage (lower right end).

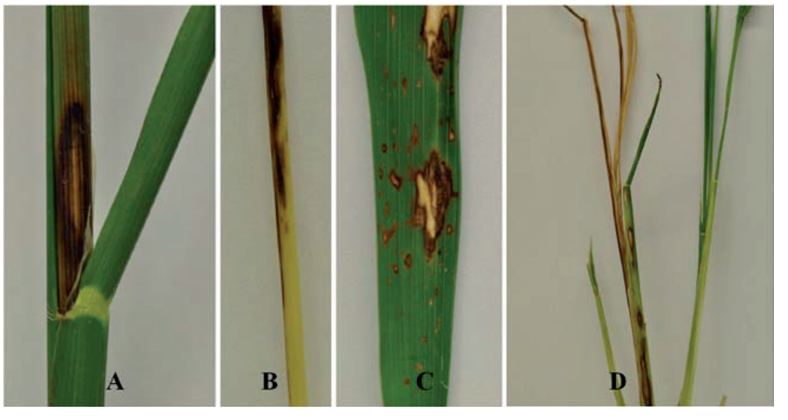

Figure 6.
Symptoms of sheath rot (A), stem rot (B), leaf lesions (C), and seedling blighting (D) caused by Burkholderia glumae in Presidio (cv) rice. Rice seedlings were inoculated with B. glumae and maintained in the greenhouse.

4. Epidemiology

The disease cycle and epidemiology of BPB of rice are not completely understood. Both *B. glumae* and *B. gladioli* species have been identified as the cause of the BPB disease. However, the former has much wider distribution in the world as shown in **Table 1**. The bacteria of both species were also found to be widely present in rice seed lots in the studies conducted in China, Japan, the Philippines, and the USA [21, 32, 48]. Therefore, infected seeds serve as the primary source of inoculum [1]. In addition, Jeong et al. [34] reported that *B. glumae* could also infect other plant species, including tomato, sesame, perilla (an herb), eggplant, and hot pepper. The bacteria are capable of inhabiting surface plants and soils under a wide range of environments [49, 50]. In a field survey conducted in Mississippi using PCR analysis, it was found that 83% of soil samples were positive for *B. glumae* and 2% of the soil samples positive for *B. gladioli* [38]. This survey also found that 85% of field irrigation water samples collected were positive for *B. glumae* and 2% of the water samples positive for *B. gladioli*. Therefore, soil and irrigation water can also serve as the sources of inoculum for the spread and development of BPB.

The bacterial pathogen invades germinated seeds, inhabits the roots and lower sheaths, and moves up the growing plant as an epiphyte (an organism growing on a plant surface, but not as a parasite) [2, 51, 52]. A recent study, using real-time fluorescence quantitative PCR to monitor the infection process of *B. glumae*, finds that the bacterium also can directly infect the rice plant by colonizing the vascular bundle of lateral roots and then spreading to upper tissues such as leaf sheaths and leaf blades through vascular system [53]. Infection by the bacterium occurs at flowering by invading rice spikelets through stomata or wound in the epidermis of glumes. The bacterium colonizes and multiplies in spikelets quickly after invasion by utilizing intermediate sugars in developing grains [51, 52]. The bacteria are spread primarily by splashing and windblown rain and panicle contact, resulting in the formation of disease foci that are frequently observed in the field [2, 54, 55].

High temperatures in combinations with high humidity or frequent rain are essential for the development of BPB epidemics. The outbreaks of BPB are usually triggered by conditions of high temperatures in combination with simultaneously high relative humidity during the heading-flowering stages. In the observations of Yokoyama and Okuhara [56], the disease developed when minimum daily temperature was ≥23°C and moderate rainfall (<30 mm/day) occurred during heading. Tsushima et al. [57] found BPB commonly occurred when relative humidity was more than 95% for 24 hours during flowering. Lee et al. [58] reported that the disease did not develop when the minimum daily temperature was less than 22°C and when relative humidity was below 80% during the heading stage. Nandakumar et al. [1] found that the optimum temperature for the growth of *B. glumae* and *B. gladioli* ranged from 35 to 40°C.

The outbreaks of BPB in the Southern USA in the epidemic years appeared to be related to unusual weather conditions. Weather conditions favorable for the development of the disease were high nighttime temperatures and high humidity or frequent rainfall during heading and flowering [10]. For example, in the 2010 epidemic year, abnormally high minimum (night time) temperatures occurred on June 21 through July 10 (**Figure 7**) when ca. 60% of the Texas rice acreage was near or at heading and flowering. During that period, rainfall was frequent and relative humidity was 95% or above most of the time (**Figure 7**). The combination of favorable weather conditions, high nighttime temperatures and high humidity, occurring at the most susceptible stages of rice plants promoted the infection and development of BPB. Similar weather patterns were observed in 1995 when a severe epidemic of BPB took place in Texas. There were many days with high maximum temperatures 35°C or

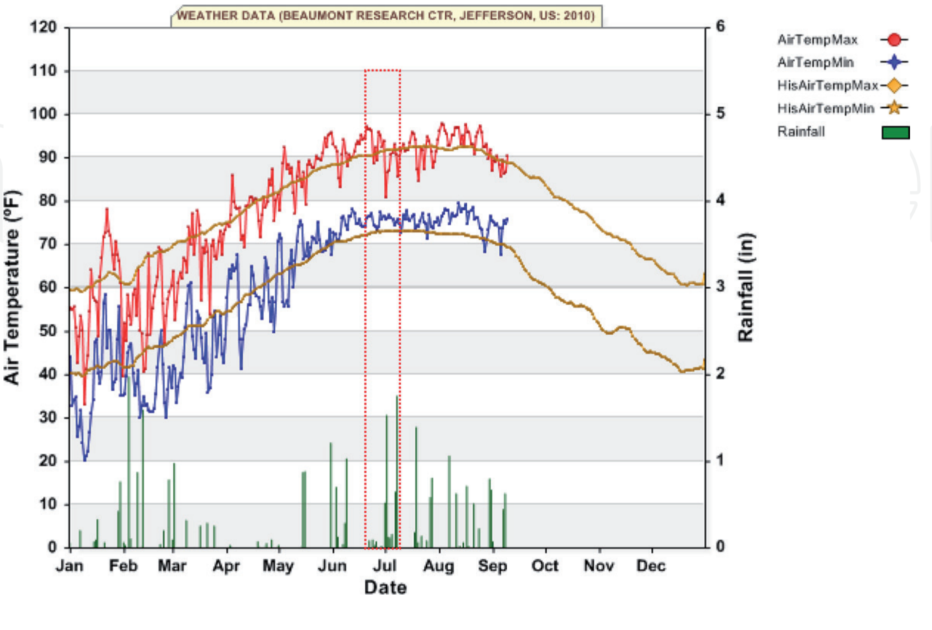

Figure 7.
Air temperatures and rainfalls during the 2010 growing season of rice at the Beaumont Center, Jefferson County, Texas. Note the red-dashed rectangle area showing minimum (night) air temperatures (blue curves) higher above the 65-year historical average (the brown curve) and frequent rainfalls (green bars). The dashed rectangle area represents the period of June 21 through July 10 that coincided with the heading and flowering stages (source: http://beaumont.tamu.edu).

Crop phenology (% heading)	Month	Week	Days				Total precipitation (cm)
			≥35°C	Mean ≥ 24°C	10 am to noon ≥32°C	Precipitation	
—	June	1	0	0	—	0	4.4
7		2	0	3	—	1	2.0
3		3	0	0	0	0	0
6		4	4	1	0	2	8.0
15	July	1	0	5	0	5	4.0
12		2	4	2	0	2	0.7
11		3	4	3	6	2	0.4
10		4	6	5	7	2	4.8
10	August	1	3	1	4	2	2.2
3		2	2	2	6	3	3.5
3		3	4	2	—	3	3.2
3		4	4	1	—	4	2.5

Table 2.
Summary of rice crops and weather data at Beaumont and Eagle Lake, Texas in 1995.

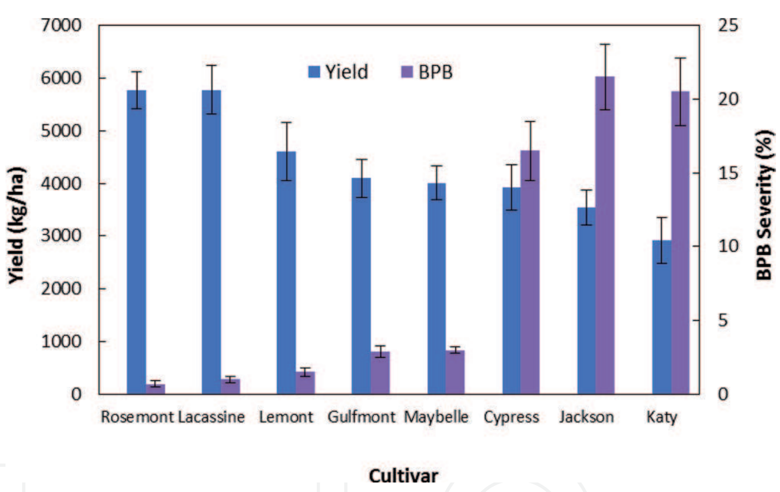

Figure 8.
Yield (left Y-axis) and bacterial panicle blight (BPB) severity (% panicles affected) (right Y-axis) of eight cultivars of rice (X-axis) in naturally infested field at Beaumont, Texas, in 1995 (source: [11]). Error bars are present in columns.

above, day temperatures above 32°C from 10 am to 12 pm (the flowering time), and precipitation from the last week of June through the first week of August (**Table 2**). Heading and flowering occurred on a large percentage of the Texas rice crop during that period. These conditions were associated with severe outbreaks of BPB and significant yield losses in 1995. **Figure 8** shows an example of the severity of this disease in 1995 and its association with yield loss for different rice cultivars, with the disease severity levels ranging from 1 to 22% of panicles affected.

5. Management strategies

Successful disease control generally relies on employing management strategies toward reducing the damage to a manageable and acceptable level. These strategies are exclusion, genetic resistance, chemical control, biological control, and cultural practice. However, for control of the BPB disease at a given geographical area, there are few management options available currently. To effectively manage rice BPB, rice producers must start with the use of pathogen-free seeds as an exclusion measure, plant with partially resistant cultivars, apply with available chemicals or biocontrol agents, and use proper cultural practice. Integrated use of these available management strategies is the key to the effective and sustainable control of the BPB disease.

5.1 Exclusion

Since the BPB disease has been reported in more than 18 countries (**Table 1**) and the disease is not present in all the rice-producing countries and regions, exclusion of the BPB pathogens from a disease-free region is the most effective strategy to prevent BPB of rice. Plant quarantine is an effective measure to achieve this goal. For example, within the USA, the state of California has employed a plant material quarantine procedure to prevent the introduction of the BPB pathogens, other rice pathogens, and weed and insect pests into the state from the southern rice-producing USA. A similar plant quarantine law has been established and enforced in China to prevent the potential importation of the BPB pathogens from foreign countries since 2007 [21].

BPB is seedborne and infected seeds serve as the primary source of inoculum [1, 2, 48]. Therefore, the use of certified seeds that are free of the BPB pathogens is another effective measure to exclude the disease from a disease-free geographic area. Different molecular detection methods including PCR that have been developed to test rice seed lots [19, 48] can aid in this process. In the USA, the use of pathogen-free seeds is recommended to manage the BPB disease. However, using PCR procedure to ensure the BPB pathogens free in certified seed has not been employed. To reduce the BPB disease, it is recommended that farmers should not use the seeds harvested from the fields that are infected with BPB the previous year.

Seed treatment can serve as the last resort to reduce and even eliminate the seedborne BPB pathogen populations and to control subsequent head disease to an accepted level. Rice seeds treated at 65°C of dry heat for 6 days can eradicate the BPB pathogens [26]. Seed treatment with the antibiotic bactericide oxolinic acid (Starner®) has been shown to control the bacterial pathogens in naturally and artificially infected seeds [59]. An antagonistic *Pseudomonas* spp. strain when applied onto seeds was effective to reduce the *B. glumae* populations in seed and suppress seedling rot [60]. Seed treatment with hot water at 60°C for 10 minutes is ineffective for control of the BPB disease although such seed treatment practice is effective to control the rice blast pathogen *M. oryzae* [61].

5.2 Genetic resistance

Considerable research efforts have been conducted globally to develop resistant cultivars as an effective and sustainable strategy for management of BPB of rice. Unfortunately, no single genes or quantitative trait loci (QTLs) for complete resistance to BPB have been found so far [13, 14]. Only several rice cultivars with partial resistance are available for commercial use. In Japan, BPB resistance breeding research efforts started as early as 1975; three partially resistant cultivars were identified through a field screening of nine cultivars and lines [62]. No resistant cultivars and breeding lines were identified in a study of screening 293 cultivars and lines using greenhouse inoculation at the flowering stage in 1983 [63, 64]. From 1985 through 2013, there were nine reported studies that screened a total of 798 cultivars and breeding lines in the field and greenhouse and identified a total of 28 cultivars and lines showing partial resistance to BPB [13, 65–73]. Most recently, Mizobuchi et al.

[74] identified two tropical *japonica* cultivars, Kale and Jaguary, with a high level of resistance and several *indica* cultivars with moderate levels of resistance. These cultivars could serve as good resistance sources to develop BPB-resistant Japanese *temperate japonica* cultivars that can be adapted for use in Japan. Most of rice cultivars commercially available in Japan are susceptible or very susceptible to the BPB disease [74].

In the USA, a collaborative research effort has been established for decades in the southern states of Arkansas, Louisiana, Mississippi, Missouri, and Texas through the Uniform Rice Research Nursery (URRN) to evaluate and develop rice cultivars with high yielding potential and resistance to BPB, sheath blight, rice blast, and other diseases. Annually, more than 200 elite breeding lines and cultivars from the southern states' breeding programs are evaluated in the URRNs inoculated with *B. glumae* at the boot to heading stages. Jupiter, a partially resistant cultivar [75–77] is usually included as a check in these multistate evaluations. Results of multiyear studies demonstrate that no complete resistance cultivars and lines are available and most of the cultivars and lines evaluated are susceptible and very susceptible to BPB [[78], Don Groth, personal communication]. However, some cultivars and lines demonstrated their partial resistance to BPB. For example, Catahoula, Jupiter, Taggart, Rondo, and XL723 (hybrid) were moderately resistant to BPB in the field evaluations conducted in Texas (**Figure 9**). Hybrid cultivars, including XL723, XL753, XL760, CLXL729, CLXL 730, and CLXL745, are relatively more resistant than most of inbred cultivars [4]. The mechanisms associated with BPB resistance in the hybrids are needed to be investigated. In addition, LM-1, a mutant line obtained from gamma radiation treatment of the susceptible cultivar, Lemont, is resistant to BPB [7, 79]. Some resistant breeding lines have been identified in the URRN evaluations in Arkansas [80].

In addition to the host resistance research that has been conducted in Japan and the USA, resistant cultivars and lines have also been reported in other countries. In Brazil, three cultivars were found to be resistant to BPB in the field evaluation [81]. In China, one cultivar, named KaohsiugS.7, was reported to show resistance to the disease when rice plants were inoculated with *B. glumae* at the flowering stage in the field [82].

Host resistance such as rice blast resistance can be broadly classified into complete and partial resistance [83]. The complete resistance is of qualitative character and race specific, which is controlled by major resistance genes (R genes). However, the partial resistance is of quantitative character and non-race specific, which is controlled by several minor genes known as quantitative trait loci (QTLs). Unlike rice blast resistance having both complete and partial resistances, it is apparent

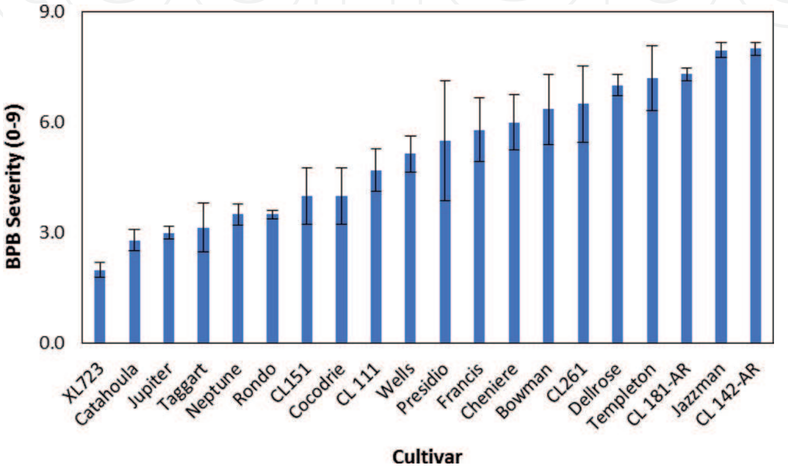

Figure 9.
Mean severities of bacterial panicle blight (BPB) (Y-axis) in 20 rice cultivars (X-axis) over two locations (Beaumont and Eagle Lake) in Texas in 2010. Error bars are present in columns.

that rice BPB resistance has only partial (quantitative) resistance and no complete resistance has been found. Pinson et al. [14] provided the first analysis of QTLs of rice resistance to BPB, using a population of 300 recombinant inbred lines (RILs) derived from a cross between Lemont and TeQing, susceptible and resistant to BPB, respectively. Lemon was an American rice cultivar, while TeQing was a cultivar from China. Twelve QTLs, namely, *qBPB-1-1*, *qBPB-1-2*, *qBPB-1-3*, *qBPB-2-1*, *qBPB-2-2*, *qBPB-3-1*, *qBPB-3-2*, *qBPB-7*, *qBPB-8-1*, *qBPB-8-2*, *qBPB-10*, and *qBPB-11*, were identified on seven chromosomes (chromosomes 1, 2, 3, 7, 8, 10, and 11). Among these QTLs, eight (*qBPB-1-1*, *qBPB-1-2*, *qBPB-2-2*, *qBPB-3-1*, *qBPB-7*, *qBPB-8-1*, *qBPB-10*, and *qBPB-11*) were derived from TeQing and four (*qBPB-1-3*, *qBPB-2-1*, *qBPB-3-2*, and *qBPB-8-2*) from Lemont. After this first report of QTL analysis in the USA, Mizobuchi et al. [73, 84] also identified one QTL, namely, RBG2, on chromosome 1, using a population of 110 backcross inbred lines (BILs) derived from a cross between Kale (resistant to BPB) and Hitomebore (susceptible) in Japan. Kale was a traditional lowland *indica* cultivar that originated from India, while Hitomebore was a modern lowland *temperate japonica* cultivar. In addition, Mizobuchi et al. [85] also have identified the first and only QTL associated with resistance to seedling rot caused by *B. glumae* from a population of 44 chromosome segment substitution lines (CSSLs) derived from a cross between Nona Bohka and Koshihikari, resistant and susceptible to seedling rot, respectively. This QTL, namely, *RBG1*, is located on chromosome 10.

The current research evidence suggests that there is no direct correlation in genetic resistance between seeding rot and grain rot caused by the same bacterium *B. glumae* [64, 73, 85].

5.3 Chemical control

Oxolinic acid (5-ethyl-5,8-dihydro-8-oxo-[1,3]dioxolo[4,5-g]quinoline-7-carboxylic acid, Starner®) is the first chemistry that has been reported to be highly effective for control of the BPB disease in rice. This antibacterial compound, a quinoline derivative, was first introduced in Japan in 1989 for control of rice seeding rot and grain rot [15]. Combined use of oxolinic acid as seed treatment and foliar sprays at heading has been reported to be the best strategy for effective control of both seeding rot and gain rot diseases [17]. When applied at the heading stage, this bactericide is highly effective to inhibit multiplication of *B. glumae* on spikelets and control the BPB disease [15, 51]. In the multiyear field trials conducted in Louisiana is Texas, oxolinic acid, when applied at the boot to heading stages, reduced BPB severity by up to 88% [86–88]. Oxolinic acid has been used three times per season for control of BPB in Japan for more than two decades [89]. Unfortunately, *B. glumae* populations resistant to oxolinic acid have been found in rice in Japan since 1998 [16, 17, 19, 89, 90]. An amino acid substitution at position 83 in GyrA (GyrA83) is responsible for the development of oxolinic acid resistance in the *B. glumae* populations [90]. It has been found that the bacterial populations resistant to oxolinic acid are also cross-resistant to other quinoline derivatives [16]. A specific PCR method has been developed to detect the oxolinic acid-resistant populations of *B. glumae* [19]. The occurrence of oxolinic acid resistance might limit its increasing use and new registrations for management of BPB in rice. Oxolinic acid is not registered for use in rice in the USA and many other countries.

Copper and copper-containing bactericides have also been reported to be effective for control of BPB in rice [86, 91–93]. These bacterial products include Kocide® 2000 (53.8% copper hydroxide), Kocide® 3000 (46.1% copper hydroxide), Previsto® (5% copper hydroxide), Badge® SC (15.4% copper hydroxide plus 16.8% copper oxychloride), Badge® X_2 (21.5% copper hydroxide plus 23.8% copper oxychloride), and Top Cop® (8.4% tric basic copper sulfate). In the field trials of Louisiana, a single application of Kocide® 2000 or Top Cop® at the boot stage reduced the BPB severity as much as 75%, and grain yield and milling quality were improved [86]. In our multiyear field trials conducted in Texas, single applications of Kocide® 3000, Badge® SC, Badge® X_2, or Previsto® at the heading stage significantly reduced BPB severity, with the reductions ranging from 42 to 96% [91–93]. However, except Previsto® with a relatively lower level of copper-active ingredient, all other copper products produced varying degrees of phytotoxicity on sprayed leaves and panicles and under certain environmental conditions reduced yields [86, 91–93]. These copper products have been registered as bactericides and fungicides for control of various bacterial and fungal diseases in citrus, tree crops, vegetables, vines, and field crop (soybeans, wheat, oats, and barley) in the USA. Probably due to their potential phytotoxicity and yield reduction, all these copper products have not been registered for management of the BPB disease on rice in the USA.

In addition to oxolinic acid and copper-based bactericides, other bactericides such as kasugamycin, probenazole, and pyroquilon are used for management of rice seedling rot and grain rot in Japan [16] and Honduras (Lex Ceamer, personal communication).

5.4 Biological control

Several studies have been conducted to develop biological control methods as a strategy for management of BPB of rice. In Japan, Tsushima and Torigoe [94] conducted the first research on the use of bacterial antagonists for control of BPB under field conditions. An antagonistic *Pseudomonas* sp. strain was found to be effective to suppress seedling rot when pretreated onto rice seeds prior to planting [60]. Furuya et al. [95] also found that rice seedling rot was reduced following seed treatment with avirulent strains of *B. glumae*. Miyagawa and Takaya [96] found that an avirulent strain of *B. gladioli* when applied onto rice panicles was very effective to reduce BPB severity. In the USA, five *Bacillus amyloliquefaciens* strains were found to be antagonistic against *B. glumae* in vitro and reduce BPB severity when applied at the heading stage in the field trials conducted in Louisiana [97]. When applied at the flowering stage, two strains of *Bacillus* sp., with antibacterial activities toward *B. glumae*, were demonstrated to reduce BPB severity by as much as 50% and increase grain yield by more than 11% in the field trials conducted in Texas [87, 88]. In a separate BPB-spread field trial study, one of the strains also showed its ability to significantly limit the spatial spread of BPB from a focal point of inoculum [55].

In addition to bacterial biocontrol agents, bacteriophages (also known as phages) have been demonstrated to be effective for management of rice seedling rot in Japan. Adachi et al. [98] found that two bacteriophages were able to lyse *B. glumae* and were highly effective to control seeding rot when rice seeds were pretreated with them. One of the bacteriophages evaluated was even more effective in reducing seeding rot than the bactericide ipconazole/copper (II) hydroxide.

5.5 Cultural practice

Few studies have been conducted to understand and develop cultural practices that could reduce the incidence and severity of BPB in rice. High levels of nitrogen fertility tend to increase the susceptibility of rice plants to the BPB disease. Avoiding excessive nitrogen rates can help reduce the damage caused by BPB. In an Arkansas study evaluating the effects of nitrogen on BPB severity, it was demonstrated that the severity of BPB at the high nitrogen rate (247 kg/ha) was 1.6 times higher than at the low rate (168 kg/ha) applied during a cropping season [99]. Under the Southern

US rice production systems, early planting or use of early maturing rice cultivars to avoid the hottest times of the growing season is another effective approach to reduce the damage caused by the disease. In addition, avoiding excessive seeding rates is also helpful in reducing the incidence and severity of the disease.

6. Conclusion and prospects

BPB has been reported in more than 18 countries and has become a global rice disease. Currently, BPB is one of the major diseases in rice in many countries, including Japan, the USA, and Latin America. The disease is highly destructive, which can cause almost complete losses in yield and milling quality under the most favorable conditions. The outbreaks of BPB are triggered by conditions of high temperatures. With predicted global warming, the disease is likely to be more prevalent on a global scale and to cause more damage in epidemic regions in the future [20, 74]. The global land and ocean surface temperature has been increased by as much as 0.85°C over the period of 1880–2012 based on the 2014 IPCC report [100]. Under the 1°C warming scenario, it is estimated that the increased damage caused by this disease in the Southern USA would result in a $103 million USD annual decrease in consumer surplus and a loss of rice production equivalent to feeding 1.9 million people (Aaron Shew, personal communication).

Effective management of this bacterial disease is challenging. Unlike most of other rice diseases, The BPB disease often develops after the heading stage, and typically no symptoms and signs can be observed before heading. Therefore, no scouting methods are currently available to detect and predict the development of the disease. No standardized seed treatment methods have been developed and commercialized specifically to eradicate or reduce the pathogen populations in rice seeds. No chemical control agents are labeled for management of the BPB disease in most countries, including the USA. The efficacy and increasing use of oxolinic acid have been affected by the development of oxolinic acid resistance in the populations of *B. glumae* in Japan and other countries. No commercially available biocontrol agents have been developed. Most of commercially available rice cultivars are susceptible or very susceptible to BPB.

Therefore, effective and sustainable control of the BPB disease largely depends on integrated use of available management options. Plant quarantine is the first defense to exclude the BPB pathogens from disease-free countries and regions. The use of pathogen-free seed or certified seed is another effective measure to control this disease. Planting with cultivars having a resistant level as high as possible is always an effective recommendation to reduce the damage caused by the disease. A limited number of rice cultivars, including hybrids, with partial resistance to BPB are available for commercial use in many countries. Since no source of complete resistance has been discovered so far, more research is needed to look for new sources of resistance through screening a greater number of germplasm lines, including those from other countries and the wild species of *Oryza*. Continued studies are needed to further characterize, fine map, or even clone the QTLs associated with BPB resistance that have been identified. More investigations are desired to understand the genetic control of BPB resistance in available resistant rice cultivars and lines, especially hybrids. These studies may lead to the development of molecular makers linked to BPB resistance that can help breeders facilitate the selection of BPB resistance in early breeding generations with more confidence. Recent advances in rice genomics and newly developed genome editing tools like CRISPR may provide new and powerful tools to better understand the mechanisms associated with BPB resistance and develop new rice cultivars with a higher level of resistance to BPB in the future. Developing and use of resistant cultivars is the best strategy to minimize the damage caused by BPB and maximize rice production in the long term.

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